Genetic Evaluation for Functional Longevity in Polish Simmental Cattle

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ABSTRACT

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The Weibull proportional hazards model was applied for genetic evaluation of functional longevity in Polish Simmentals. Data consisted of production and disposal records for 12 527 Simmental cows, daughters of 294 sires, calving for the first time from 1995 to 2014 in 286 herds. Length of productive life of cows was calculated as number of days from the first calving to culling or censoring. Average length of productive life of 4462 cows with complete (uncensored) survival records was 1198 days (39.3 months); mean censoring time for the remaining 8065 cows was 1093 days (35.8 months). Functional longevity was defined as length of productive life corrected for production. The model included time-independent fixed effect of age at first calving, time-dependent fixed effects of year-season, parity-stage of lactation, annual change in herd size, relative fat yield and protein yield, and random herd-year-season and sire effects. Likelihood ratio tests showed a highly significant impact of all fixed effects on longevity, except for relative fat yield. Estimated sire variance was 0.069, resulting in the equivalent (accounting for censoring level) heritability of 0.09. Standardized relative breeding values (RBV) ranged from 71 to 139 (mean 101.4, SD 9.12). Average reliability of RBVs was 0.47. Moderate heritability supports the possibility of effective selection for functional longevity, which will be included in the total selection index for Polish Simmentals.

Keywords: cattle; Polish Simmentals; productive life; Weibull proportional hazards model

Polish Simmental cattle is a dual-purpose breed which makes up about 1% of the Polish cow population. In recent years this breed has gained popularity due to its beef quality and good milk production. Length of productive life (LPL) is the most important trait determining the profitability of dual-purpose cattle production. Longer herd life is positively related to a lower rate of costly replacements and to higher production due to the

greater proportion of mature cows (VanRaden and Wiggans 1995).

In cattle production systems, culling of cows can be involuntary when it is caused by fertility problems, health problems and accidents, or voluntary, most often due to low production. Reduction of involuntary culling allows more intensive voluntary culling, leading to higher profit (Van Arendonk 1985). Ducrocq et al. (1988) described

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two kinds of longevity: true longevity (i.e. the cow's ability to delay any culling) and functional longevity (the ability to delay involuntary culling only). Functional longevity is measured as LPL corrected for production, which is the main criterion for voluntary culling (Ducrocq et al. 1988; Vukasinovic et al., 1997, 2001).

Routine genetic evaluations of longevity are frequently performed using survival analysis, the Weibull Proportional Hazards model being the most frequent approach (Interbull 2016). This approach has some advantages over linear models. Survival analysis accounts for censored (still in production) and uncensored (culled) data, and allows inclusion of environmental time-independent factors such as age at first calving, as well as time-dependent effects such as level of milk yield and its components, lactation number, lactation stage, herd, year and season of calving, herd size or herd size variation (Ducrocq 1994; Vukasinovic et al. 2001; Weigel et al. 2003; Strapakova et al. 2013).

The purpose of this study was to use survival analysis to assess changes in the risk of culling related to environmental factors affecting the functional longevity of Polish Simmental cows, and to estimate genetic parameters. We present a model that will be implemented in routine sire breeding value estimation.

MATERIAL AND METHODS

Data. Test-day production, lactational production and disposal records of Simmental cows from the SYMLEK National Milk Recording System were used. Records with incorrect calving or culling dates, age at first calving outside the range of 18–48 months, and missing sire identification were removed. A criterion of minimum 15 daughters per sire and 15 cows per herd was imposed. After editing, records were available for 12 527 cows from 286 herds, which calved for the first time between 1995 and 2014. Cows were daughters of 294 sires. LPL of a cow was measured as the number of days from the first calving to culling (uncensored records) or last test day (censored data). The censoring criterion was based on the reasons for culling registered in the SYMLEK system. A lifetime record was considered to be completed (uncensored) if the cow was culled for a reason other than being "sold for dairy purposes". Longevity records for cows with code "sold for dairy purposes" or without culling code were considered as censored. Functional longevity was defined following Ducrocq et al. (1988) as LPL corrected for within-herd-year-season phenotypic production of a cow. The average LPL of 4462 cows with complete (uncensored) survival records, representing 36% of the population under study, was 1198 days (39.3 months). Mean censoring time for the remaining 8065 cows with censored data was 1093 days (35.8 months). Maximum culling and censoring time was 5046 and 4975 days (165.4 and 163.1 months), respectively.

Statistical model. We studied LPL using survival analysis methodology. The hazard function describing the risk of culling of cows (daughters of bulls) at time t was modelled using the Weibull proportional hazards (PH) sire model. The hazard function was the product of a time-dependent baseline hazard function related to the ageing process and an exponential function of the explanatory variables affecting culling rate.

In this study the following Weibull model was used:

$$h(t) = h_0(t)\exp[age + ys(t) + ls(t) + hsize(t) + fat(t) + prot(t) + hys(t) + sire]$$
(1)

where:

t = time from first calving to culling or censoring

h(t) = hazard function for a cow at time t

 $h_0(t)$ = Weibull baseline hazard function with scale parameter λ and shape parameter ρ :

$$h_o(t) = \lambda \rho(\lambda t)^{\rho - 1} = \rho t^{\rho - 1} e^{\rho \ln \lambda}$$
 (2)

The fixed effects included in the model were:

age = time-independent effect of age at first calving with 22 classes, including the age < 20 months class, 20 one-month classes of age between 20 and 40 months, and age ≥ 40 months as $22^{\rm nd}$ class

ys = time-dependent fixed effect of year-season of calving (years 1995–2014; 2 seasons, April– September and October–March)

ls = time-dependent combined effect of lactation number from 1 to 6 (lactations 6 and later were pooled) and 4 stages of lactation demarcated by days 30, 180, and 305 of each lactation

hsize = time-dependent effect of yearly herd size variation with classes reflecting the relative change of herd size from the current year to the next year

 $(<-50\%, -50 \text{ to } -31\%, -30 \text{ to } -11\%, -10 \text{ to } 9\%, 10 \text{ to } 29\%, 30 \text{ to } 49\%, \ge 50\% \text{ change})$

fat, prot = time-dependent effects of classes of 305-day
 fat and protein production levels relative to
 herd mean

The classes defined separately for the first and later lactations were: class 1 – production more than 50% below herd mean; 10 classes of production falling within the ranges set by border points at –50%, –40%, –30%, –20%, –10%, 0%, 10%, 20%, 30%, 40%, and 50% of herd mean; and class 12 representing production more than 50% above herd mean.

The fat and protein yield as the main production selection criteria in Polish Simmentals were included in the model to approximate functional longevity.

The random effects included were:

hys = time-dependent effect of herd-year-season, assumed to be independently distributed, following a log-gamma distribution

sire = genetic effect of sire of cow, assumed to follow a multivariate normal distribution with mean zero and variance $\mathbf{A}\sigma_s^2$ (where σ_s^2 = sire variance and \mathbf{A} = relationship matrix)

The random *hys* effect represented the withinherd yearly and seasonal differences in culling intensity, while the fixed year-season factor was included in the model to account for the overall changes in culling risk associated with calendar time.

Estimation. Computations were done using the software package Survival Kit, Version 6.12 (Meszaros et al. 2013b). In the first step, the significance of the fixed effects was evaluated using the reduced model without random effects. The generalized coefficient of determination \mathbb{R}^2 of Maddala (1986) was used to determine the proportion of total variation explained by the model:

$$R_{\text{Maddala}}^2 = 1 - (L_0/L_M)^{2/n} \tag{3}$$

where:

n = sample size

 L_0 = value of the likelihood function for a model with no predictors

 $L_{\scriptscriptstyle M}$ = likelihood for the full model

The significance of fixed effects and their overall impact on longevity were checked by a series of likelihood ratio tests comparing the model tested with a model excluding one effect under testing at a time. The influence of each factor on longevity was analyzed based on its contribution to the log-likelihood function.

In the next step, the Weibull distribution parameters (ρ, λ) , hys distribution parameter (γ) , and the variance of sire effect (σ_s^2) were estimated using the full model including all, except the non-significant fat yield, fixed and random effects. The random hys effect was algebraically integrated out and was not used in heritability approximation; the γ parameter was estimated jointly with other effects.

Based on the sire genetic variance estimate (σ_s^2) , effective (h_{eff}^2) and equivalent (h_{equ}^2) heritability were calculated according to Yazdi et al. (2002):

$$h_{\text{eff}}^2 = 4 \times \sigma_s^2 / (\sigma_s^2 + 1)$$
 (4a)

$$h_{\text{equ}}^2 = 4 \times \sigma_s^2 / (\sigma_s^2 + 1/p)$$
 (4b)

where:

p = proportion of uncensored records

The solutions for fixed class effects were expressed as a relative risk of culling (RRC) defined as the ratio of the estimated risk of a cow being culled under the influence of a specific level of a particular factor to the arbitrary chosen reference risk, with other factors assumed to be constant.

The solutions for sire effect were obtained from the same model. They were standardized, relative to the base, on an average of 100 and a standard deviation of 10 (with the sign reversed) to give the sire relative breeding value (RBV). The following formula was used:

$$RBV = \{[(s - mean_base)/sd_base] \times (-10)\} + 100 (5)$$

where:

RBV = relative breeding value of a sire s = solution for a particular sire

mean_base = mean solution in the group of base sires
sd_base = standard deviation of solutions of base
sires

Higher RBV means better breeding value representing a lower risk of culling of bulls' daughters. The genetic reference base used for the standardization consisted of bulls with breeding value reliability of at least 50%.

The reliability (REL) of sire BV was calculated using the following formula (Ducrocq 1999; Vukasinovic et al. 2001):

Table 1. Likelihood ratio tests comparing full model with models excluding one effect at a time

Effect excluded	Δdf	χ^2 (-2 × LogL change)	$P > \chi^2$
Lactation number × stage of lactation	23	1770.4	< 0.0001
Age at first calving	21	45.9	< 0.0001
Year-season	27	644.4	< 0.0001
Annual change in herd size	8	69.5	< 0.0001
305-day fat production	13	15.1	0.2989
305-day protein production	13	158.2	< 0.0001

df = degrees of freedom, χ^2 = chi-square statistic, LogL = log-likelihood function, P = probability

$$\begin{aligned} \text{REL} &= (\frac{1}{4} \times \text{REL}_{\text{gsire}} + \text{REL}_{\text{prog}} - 2 \times \frac{1}{4} \text{REL}_{\text{gsire}} \times \\ &\times \text{REL}_{\text{prog}} / (1 - \frac{1}{4} \times \text{REL}_{\text{gsire}} \times \text{REL}_{\text{prog}}) \end{aligned} \tag{6}$$

where:

$$\begin{aligned} \text{REL}_{\text{prog}} &= \text{N}_{\text{prog}} / \{ \text{N}_{\text{prog}} + [(4 - h^2)/h^2] \}, \\ \text{REL}_{\text{gsire}} &= \text{N}_{\text{gsire}} / \{ \text{N}_{\text{gsire}} + [(4 - h^2)/h^2] \} \end{aligned}$$

where:

 N_{prog} = number of uncensored daughters of a sire N_{gsire} = number of uncensored daughters of sires' sire $h^2 = h_{eff}^2$ = effective heritability

RESULTS

The estimate of Weibull distribution shape parameter ρ was 2.25, and the intercept $\rho \log \lambda$ was -15.14. These two parameters define the baseline hazard function (Eq. 2); an estimated value of ρ greater than 1 indicates that hazard increases with time.

The R^2 of Maddala, showing the proportion of total variation explained, was 0.56. All fixed effects except fat yield were highly significant (P < 0.0001). The largest overall influence on LPL, measured by the contribution to the log-likelihood function (Table 1), was found for the combined effect of lactation number and stage of lactation. The second important factor was year-season, followed by within-herd protein production, annual herd size change, and age at first calving. Within-herd fat production, which was not significant, made a very small contribution to the likelihood function. The fat production effect was then excluded from the model; additional likelihood ratio tests confirmed the significance of other fixed effects.

Factors affecting longevity

Relative risk of culling. The solutions for fixed class effects expressed as relative risks of culling (RRC) describe the details of the relationship

between a particular effect and longevity (Figures 1–5). Based on the RRC values, the influence of different classes of the effect on culling risk could be compared. The lowest RRC indicates the optimal class in relation to longevity.

Lactation number \times stage of lactation. The RRC values for classes of the lactation number \times stage of lactation interaction effect are presented in Figure 1. Generally, RRC was the highest in the first lactation and decreased slightly in later lactations, but this does not necessarily mean that in later lactations the overall risk of culling is lower, because the effect of lactation number only modifies the baseline hazard function, which increases with ageing of an animal. Within lactations we observed two different patterns for culling risk. In the first lactation the risk was highest in the first stage of lactation (0–30 days). It was more than twice higher than in the second stage (30–180 days), and more than three times higher than in the third

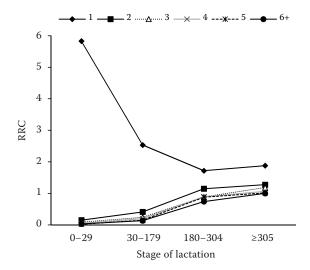


Figure 1. Relative risk of culling (RRC) by lactation \times stage of lactation (lactations: 1 to 6+; stage: 0–29, 30–179, 180–305, more than 305 days)

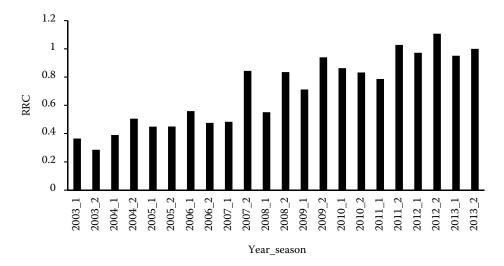


Figure 2. Relative risk of culling (RRC) by year-season (years 2003–2013; seasons: 1 – spring and summer, 2 – autumn and winter)

stage (lowest risk, 180–304 days), compared to which the risk after 305 days was only slightly higher. Within the second and later lactations, the risk of culling rose from extremely low in the first stage and still very low in the second stage of lactation to almost six times higher after 180 days of lactation. The differences within lactations were greater than between lactations.

Year-season. The fixed year-season factor was included in the model to account for the overall changes in culling risk associated with calendar time.

Figure 2 shows the upward trend in RRC estimates for consecutive year-season classes. In 10 years RRC increased more than twofold. We found some seasonal differences, especially since 2007, with the risk of culling being higher in autumn and winter.

Fat and protein production level. Our tests showed that the protein production level was the third important factor influencing LPL (Table 1). The shape of this relationship is presented in Figure 3. RRC for cows producing less than 40% of herd mean was about five times higher than for

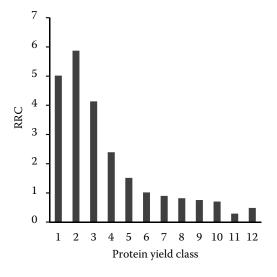


Figure 3. Relative risk of culling (RRC) by within-herd-year-season classes of the 305-day protein yield level relative to herd mean (1: < -50%, 2: -50 to -41%, 3: -40 to -31%, 4: -30 to -21%, 5: -20 to -11%, 6: -10 to -1%, 7: 0 to 9%, 8: 10 to 19%, 9: 20 to 29%, 10: 30 to 39%, 11: 40 to 49%, 12: $\geq 50\%$)

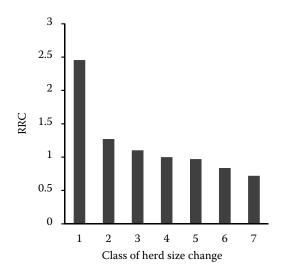


Figure 4. Relative risk of culling (RRC) by the classes of yearly herd size change (class 1: <-50%, 2: -50 to -29%, 3: -30 to -11%, 4: -10 to 9%, 5: 10 to 29%, 6: 30 to 49%, 7: $\geq 50\%$ change)

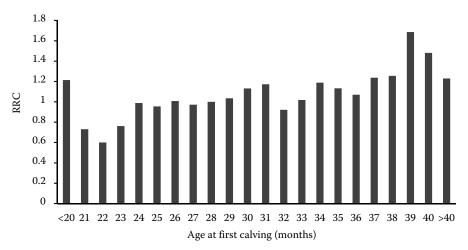


Figure 5. Relative risk of culling (RRC) by age at first calving (months)

cows with average production. Then the culling risk decreased sharply with protein yield rising toward the herd average. A further increase of protein production resulted in a moderate reduction of risk; high-producing cows had a lower risk than average producers, by up to 50%. The RRC estimates for fat yield classes showed no particular pattern.

Annual herd size change. The influence of annual change of herd size on culling risk is shown in Figure 4. Generally the risk of culling was higher when herd size decreased and lower when it increased. Cows in herds whose size declined by more than 50% were at a risk of culling about 2.5 times higher than cows in herds changing size by no more than 10%, whereas the risk of culling in herds decreasing by 30–50% and 10–30% was correspondingly by only 27% and 10% higher. In herds whose size increased by 10–30%, 30–50%, or more than 50%, the risk of culling cows was lower respectively by 3%, 20% and 40%, compared to herds with less than a 10% change in the number of cows.

Age at first calving. Age of cow at first calving was found to be a significant factor influencing culling risk, but its impact was small (Table 1). The RRC estimates showed an increasing trend for age 22–40 months (Figure 5). For the oldest first-calvers the culling risk was almost two times higher than for the young ones, with the exception of cows calving for the first time before 20 months of age. These youngest cows were up to 40% more likely to be culled than cows calving in the period of 21–23 months, the optimal (low RRC) period in terms of longevity.

Hys effect. The random herd-year-season effect accounts for within-herd yearly and seasonal

changes of culling policy. The solutions for this effect were of no interest in our study and it was algebraically integrated out. The γ parameter of the *hys* distribution, estimated jointly with other effects, amounted to 1.36 (Table 2).

Genetic effect. The estimated sire variance was 0.069, which resulted in effective heritability of 0.25, and equivalent heritability of 0.09 (Table 2). The solutions for sire effect expressed as RRC (exponent of solutions on original logarithmic scale) ranged from 0.524 to 1.724 (mean 1.024, SD 0.16). RBV ranged from 71 to 139 (mean 101.4, SD 9.12). Figure 6 shows average RBV by year of birth of bulls. We noted a slight positive genetic trend: average RBV for bulls born between 1993 and 2008 increased by about 0.4% per year. The average reliability of sire breeding values was 0.47. Average reliability was lower in younger bulls (Figure 6).

Table 2. Weibull and herd-year-season (*hys*) effect distribution parameters, sire variance, and heritability estimates

Parameters	Estimates			
Weibull distribution parameters				
ρ	2.25			
$\rho log \lambda$	-15.14			
Distribution parameter of hys (γ)	1.36			
Sire variance (σ_s^2)	0.069			
Heritability on log scale (h_{\log}^2)	0.16			
Effective heritability (h_{eff}^2)	0.25			
Equivalent heritability (h_{equ}^2)	0.09			

 ρ = estimate of Weibull distribution shape parameter, $\rho log \lambda$ = intercept

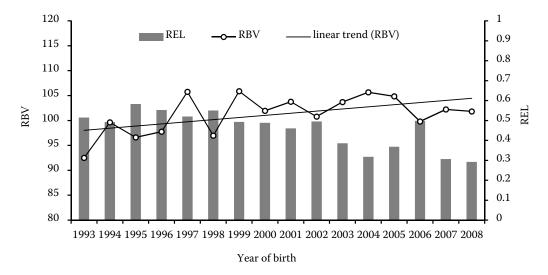


Figure 6. Mean relative breeding value (RBV) and reliability (REL) by birth year of bulls (1993–2008)

DISCUSSION

Survival analysis is the method of the first choice for genetic evaluations of functional longevity in dairy cattle. In this study we used the Weibull proportional hazards model to analyze factors affecting LPL and to estimate the genetic parameters and sire breeding values of functional longevity in Polish Simmentals. The hazard function modelled was the product of a baseline hazard function defined by two Weibull distribution parameters and a function of the explanatory variables, i.e. the environmental and genetic effects. Our estimates of Weibull parameters, the shape parameter (ρ) 2.25 and the intercept ($\rho \log \lambda$) -15.14, were in the range of values reported by Sasaki (2013) for longevity traits in dairy cattle, and were similar to results obtained for Simmental populations (Jovanovac et al. 2013; Raguz et al. 2014). Such values of these parameters (with $\rho > 1$) demonstrate the age-linked increase of cows' culling risk.

Environmental factors. Among the environmental fixed factors included in the model, the combined effect of lactation number and stage of lactation had the highest impact on culling risk. The high RRC in the first lactation was clearly lower in later lactations and decreased slightly with increasing lactation number (Figure 1), in agreement with other studies (Ducrocq 1994; Vukasinovic et al. 2001; Egger-Danner et al. 2005; Meszaros et al. 2013a; Strapakova et al. 2013). Our results are also in line with published findings that the risk of culling changes significantly within lactation,

although the exact partitioning of lactations differs among studies. RRC in the first lactation has been reported to be the highest at the beginning, low in the middle, and slightly higher at the end; and in later lactations it has been found to be very low at the beginning and the highest at the end (Vukasinovic et al. 2001; Egger-Danner et al. 2005; Pachova et al. 2005; Meszaros et al. 2013a). This is similar to our results. In contrast, Bielfeldt et al. (2006) and Strapakova et al. (2013) reported an uptrend of culling risk within all lactations. The high risk at the end of a lactation has been explained by the practice of postponing culling until production declines or when it is known whether the cow is pregnant, while the high risk of culling in the first stage of the first lactation might reflect the specific selection criteria for first-lactating cows (Vukasinovic et al. 2001; Meszaros et al. 2008). Greater differences in culling risk within rather than between lactations, which we observed, were also found by Roxstrom and Strandberg (2002) or Bielfeldt et al. (2006).

The year-season effect is included in models used in genetic evaluations of longevity to reflect different culling policies in populations across years (Bielfeldt et al. 2006; Jovanovac et al. 2013). In this study the year-season effect was the second most important factor influencing LPL. The upward trend, resulting in an almost twofold increase of the RRC in the ten-year period, can be explained in part by the cumulative effect of increasing milk yield per cow during that time, which led to increased culling to keep overall herd production

under the milk quota limits. The higher culling risk observed in winter may also be related to the quota system. Bielfeldt et al. (2006) and Ducrocq (1999), who also found higher risk in winter, attributed this result to higher intensity of culling at the end of each quota year.

Production level is often cited as a principal reason for voluntary culling and consequently one of the most important factors affecting cow longevity (Weigel et al. 2003; Sewalem et al. 2005; Meszaros et al. 2008). In models used for genetic evaluations of functional longevity, the production effect is expressed as classes of within-herd relative milk or fat or protein yields. Researchers generally agree that the risk of culling increases with decreasing production. The culling risk for Holstein cows having milk yield at about 1.5 or 2 standard deviations below the herd average has been reported to be even five times higher than for cows with average production (Durr et al. 1999; Pachova et al. 2005). The same studies showed that production above the herd average results in a moderate decrease of the culling risk. Meszaros et al. (2008) gave similar estimates for Slovak Pinzgau cows. For some other Simmental populations a slightly weaker effect of low milk production was found (Jovanovac et al. 2013; Strapakova et al. 2013). Apart from milk yield, low fat or protein production have also been found to increase the culling risk (Vukasinovic et al. 2001; Egger-Danner et al. 2005; Bielfeldt et al. 2006; Chirinos et al. 2007). In our model the within-herd production level of a cow was represented by relative-to-herd-average fat and protein yields, which are components of the selection index used in Polish Simmentals. Our results for the protein effect - high risk of culling for cows with low relative yield, decreasing with the increase of production - are in accord with other published results (Chirinos et al. 2007). The relative fat yield effect was not significant in this study, and the RRC estimates showed no particular pattern. This may reflect the use of a protein-tofat ratio of 2:1 in the production selection index. The fat production effect was excluded from the model for genetic evaluation of longevity in Polish Simmentals.

Another factor that affects the risk of culling is yearly change of herd size. We found that an annual decline in herd size of more than 50% was associated with a substantial increase of culling risk; the risk was 2.5 times higher than for stable-

size herds. On the other hand, an increase of herd size resulted in only a slight decrease of culling risk. Our estimates of risk are close to those given by Meszaros et al. (2008) and slightly higher than those from some other authors (Ducrocq 1999; Egger-Danner et al. 2005; Chirinos et al. 2007; Strapakova et al. 2013). Durr et al. (1999) and Sewalem et al. (2005) reported a higher culling risk for both decreasing and increasing herd size. In general, the effect of herd size change reflects differences in culling policy between expanding and shrinking herds.

Age at first calving is considered to be of minor importance to dairy cows' longevity. Some authors reported that it had a slight effect on culling risk (Durr et al. 1999; Vukasinovic et al. 2001; Pachova et al. 2005; Meszaros et al. 2008) and others have found it to be nonsignificant (Ducrocq 1994). Most studies have shown a tendency to shorter LPL in cows calving for the first time at older age, and it has been suggested that late calvings are related to poor fertility or other health problems which also affect longevity (Vukasinovic et al. 2001; Pachova et al. 2005; Sewalem et al. 2005; Strapakova et al. 2013; Zavadilova and Stipkova 2013). Sewalem et al. (2005) found a higher risk of culling for cows calving for the first time below 21 months of age and suggested that it could be due to a greater risk of dystocia in younger cows. Jovanovac et al. (2013) gave different results for Croatian Simmentals. They noted a slightly higher risk of culling for cows calving for the first time at lower age, but the differences in risk ratios across all age classes were very small. In our study the effect of age at first calving on longevity was significant, but was the lowest of all the analyzed environmental effects. We found increased risk of culling for older first-calvers and for the youngest cows calving for the first time below 20 months of age. Optimal age in terms of longevity, i.e. associated with the lowest RRC, was 21-23 months. Similarly, in Slovak Simmentals, Strapakova et al. (2013) found that the risk of culling was the lowest for the class of 600-778 days at the first calving. This is in line with recommendations in the literature (Gill and Allaire 1976; Zavadilova and Stipkova 2013).

Genetic effect. The different trait definitions (e.g. total lifetime, true productive life, functional productive life, number of parities, lifetime days in milk, survival to fixed age) and the different methods used in genetic evaluation of longevity

based on linear, random regression, threshold, or proportional hazards (PH) models produce a wide range of heritability estimates (0.01–0.22); linear models yield lower estimates (0.01–0.10) (Sasaki 2013; Imbayarwo-Chikosi et al. 2015). Survival analysis, which provides a better description of longevity data than other models do, leads to more complete extraction of genetic variance and thus higher heritability estimates (Vukasinovic et al. 1999).

With Weibull models heritability can be expressed on a logarithmic or original scale. Heritability on a logarithmic scale lacks a biological interpretation (Ducrocq 1999) and cannot be compared directly with heritability obtained from linear models. In view of this, a few approximate formulas for heritability on an original scale have been proposed, which are also used for calculations of breeding value reliability (Ducrocq 1999; Yazdi et al. 2002). According to Sasaki review (2013), estimates of heritability expressed on an original scale (effective heritability) range from 0.04 to 0.20 and usually are higher than those expressed on a logarithmic scale (0.02-0.116). In our study, calculated based on a sire variance estimate of 0.069, the effective heritability was 0.25. Such a result was above the range reported for other populations by Sasaki (2013). Our estimate of effective heritability was only slightly higher than the heritability of 0.23 reported for Czech Simmentals (Interbull 2016). The equivalent heritability (0.09; Table 2) accounting for the level of censoring (Eq. 4b), was higher than heritabilities between 0.06 and 0.08 reported in other studies of Simmental cattle longevity (Jovanovac et al. 2013; Strapakova et al. 2013; Raguz et al. 2014). The moderate heritability supports the possibility of selection for functional longevity in Polish Simmentals.

Reliable breeding values are the basis for selecting the best animals. In survival analysis, sire breeding values are estimated using longevity data from censored and uncensored daughters, while the reliability of EBVs – a measure of the accuracy of the evaluation – is approximated based on heritability (which in the case of longevity is low) and on the number of uncensored (culled) daughters only (Ducrocq 1999). The resulting problem of low reliability of longevity breeding values, especially in young animals, has been discussed by many authors (e.g. Ducrocq 1994; Vukasinovic et al. 2001). Investigating the impact of censoring on

breeding value accuracy and sire ranking, Vukasinovic et al. (1999) showed that a high proportion of censored records reduced evaluation accuracy. In our study, reliability was increased somewhat by applying the formula (6) based not only on the number of the bull's own uncensored daughters but also on a pedigree information. Still, the average reliability of sire breeding values was only 0.47, and it was lower for younger bulls. In our data the level of censoring is rather high (64%). Jovanovac et al. (2013) reported similar average reliability of 0.49 for Croatian Simmental bulls, Strapakova et al. (2013) found a lower value of 0.34 for Slovak Simmentals, and Meszaros et al. (2008) gave even lower mean reliability of 0.25 for Slovak Pinzgau cattle, although the censoring levels reported in these studies were lower (below 30%). Generally, as heavily influenced by numbers of daughters, low average reliabilities in small populations would be expected.

The rules for breeding value publication are often based on some minimum reliability requirement (Interbull 2016). Our criterion of reliability no lower than 0.2 was met by 279 of the total 294 evaluated sires. Any criterion based on higher reliability will obviously reduce the number of bulls whose breeding value may be published. A method commonly used to increase the reliability of breeding values is to construct a combined longevity index based on genetically correlated traits - early predictors of longevity (Weigel et al. 1998). This is worth considering for genetic evaluation of longevity in the Polish Simmental population. It will require further research aimed at estimating the genetic correlations of longevity with other functional traits.

CONCLUSION

In this study the combined effect of the lactation number and stage of lactation had the largest overall impact on functional longevity of Polish Simmentals. The risk of culling was higher in the first stage of the first lactation and in the last stages of all lactations. Year-season had a moderate impact, followed by protein production, annual herd size change, and age at first calving. The within-herd fat production effect was not significant. The risk of culling was high for cows with low within-herd-year-season protein production, cows from herds

of decreasing size, and cows calving for the first time at older age. The risk of culling has increased in recent years, with higher values in autumn and winter than in spring and summer.

The moderate (equivalent – accounting for censoring level) heritability value of 0.09 supports the possibility of selection for functional longevity in Polish Simmentals.

The Weibull proportional hazards model, the one we used here, will be recommended for routine genetic evaluation. Functional longevity will be included in the total selection index for Polish Simmentals.

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